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CO_2 efflux from leaf litter focused on spatial and temporal heterogeneity of moisture

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Abstract

Leaf litter respiration (R_{LL}) was directly measured in situ to evaluate relationships with the water content in leaf litter (WC), which is distributed heterogeneously under natural conditions. To do so, we developed a small, closed static chamber system using an infrared gas analyzer, which can measure instantaneous R_{LL}. This study focuses on the measurement of CO_2 effluxes from leaf litter using the chamber system in the field and examines the relationship between R_{LL} and WC among seven broadleaf species in a temperate forest. The measurements focused on the position of leaves within the litter layer, finding that both R_{LL} and WC were significantly higher in the lower layer. The value of R_{LL} increased with increasing WC, and the response of R_{LL} to WC was similar among all seven species. Moreover, the temporal variation in WC differed among three species and was associated with leaf litter thickness. The observed heterogeneity in WC induced by the physical environment (e.g., position and thickness of leaf litter) affects the variation in WC and therefore both R_{LL} and the decomposition rates of organic matter in the litter layer.

Keywords Leaf litter respiration・Litter decomposition・Moisture・Spatial and temporal variation・Soil respiration

Introduction

The litter layer (L layer) usually includes most of the labile carbon and most of the microbial biomass held in forest soil (Snajdr et al. 2008). The CO_2 efflux from the L layer is one of the main sources of heterotrophic respiration and soil respiration. Hosoe et al. (2005) reported that the contribution to soil respiration of the CO_2 efflux from the L layer could reach approximately 27% in a larch forest in central Japan. And, the CO_2 efflux from the L layer is strongly controlled by moisture conditions. For example, Cisneros-Dozal et al. (2007) reported that the contribution to soil respiration of the CO_2 efflux rate from the L layer varied between 5 and 37% in response to water additions in a temperate deciduous forest in the United States. The CO_2 efflux from the L layer varies over short periods of time (a few minutes to days), followed by rapid changes in the environmental conditions of the litter itself (e.g., litter water content, temperature) (Borken et al. 2003; Cisneros-Dozal et al. 2007). In particular, the frequency of the wetting and drying of litter may affect the total CO_2 efflux rate from the L layer on the forest floor.

The moisture status of the L layer experiences more dynamic wetting and drying processes than the lower soil layer, associated with precipitation and evaporation (Hanson et al. 2003; Jomura et al. 2012). Simard and Main (1982) showed that leaf litter off the ground (the upper layer) is directly exposed to wind and therefore dries more quickly than leaf litter on the ground (the lower layer). The moisture status strongly affects microbial activity, resulting in variation of heterotrophic respiration (Bunnell et al. 1977; DeForest et al. 2009). Therefore, the vertical distribution of leaf litter moisture status inside the L layer would affect the decomposition rate. To examine the characteristics of CO_2 efflux from the L layer, detailed and in situ

measurements of the distribution of moisture status and leaf litter respiration inside the L layer are required.

In this study, we developed an easy-to-use chamber system which allow us to measure instantaneous CO_2 efflux rates from small leaf litter sample in the field immediately following sampling. We measured leaf litter respiration (R_{LL}) and leaf litter water content (WC) focusing on the vertical position of leaf litter within the L layer, and examined the relationship between R_{LL} and WC within the L layer among seven temperate broadleaf species. We also examined the temporal variations in WC and R_{LL} among three species based on litter thickness. From these data, we inferred how physical environments (position and thickness of leaf litter) influence the variations in WC and R_{LL}.

Materials and Methods

1 Site description

This study was conducted in two adjacent temperate forests located in the Botanical Gardens, Faculty of Science, Osaka City University, Japan (34°76' N, 135°70' E) at 40–120 m elevation above sea level. Forestation was carried out in the garden for monitoring biomass changes in the 1960s. The sites selected consisted of one deciduous (1.0 ha) and one evergreen broadleaf forest (1.5 ha). The dominant species in the deciduous forest was *Quercus serrata* (*Qs*), and the evergreen forest was composed of a mixture of *Castanopsis sieboldii* (*Cs*), *Lithocarpus edulis* (*Le*), *Machilus thunbergii* (*Mt*), *Quercus myrsinaefolia* (*Qm*), *Quercus glauca* (*Qg*), and *Ilex integra* (*Ii*).

Annual mean temperature and precipitation from 1981 to 2010 were 15.6°C and 1,324 mm, respectively, which were observed at the nearest weather station (AMeDAS, Japan Meteorological Agency, Hirakata), 5.2 km away from the botanical garden. In the study area, June and July are the rainy season, while August is the driest month. August also had the highest temperature over the study period. Monthly mean temperatures in August 2009 and 2010 were 27.4°C and 30.1°C, respectively.

2 Measurement system of R_{LL}

R_{LL} was measured using a static closed-chamber system. The system consisted of an infrared gas analyzer (IRGA, GMP343; Vaisala Group, Vanta, Finland) attached to a small cylindrical chamber, was powered by a portable battery (14.8 V), and was suitable for measuring the respiration rate of small leaf litter samples. Chambers of three different volumes (0.308 L, 0.375 L, and 0.541 L) were selected according to the available sample sizes. The interior temperature of the chamber was measured with a

copper-constantan thermocouple.

The CO_2 concentration and temperature inside the chamber were recorded at 1-s intervals using a data logger (GL200A; Graphtec, Kanagawa, Japan). The measurement period for each sample was approximately 10 min. R_{LL} was calculated from the measured increase in CO_2 concentration using a linear regression of the linear portion of the resulting data. The IRGA response to a change in CO_2 concentration had a time lag of several tens of seconds due to the permeability of the air filter attached to the sensor and increased rate of CO_2 concentration per unit time was unstable within one minute after that. Therefore, data from the first 3 min were discarded to maintain high quality data collection. The respiration data for the middle 5-min period were used to calculate leaf litter respiration by the following equation:

$$R_{LL} = \Delta C_{CO2} \times \frac{V}{V_{air}} \frac{273.2}{273.2 + T} \frac{M_{CO2}}{DW} \times 60^2, \quad (1)$$

where R_{LL} ($mgCO_2\ kg^{-1}\ h^{-1}$) is CO_2 efflux from the leaf litter; ΔC_{CO2} is the increased rate of CO_2 concentration per unit time (CO_2 ppm s^{-1}); V(L) is the volume of the system; V_{air} is the standard gas volume (22.41 L mol^{-1}); T is temperature inside the chamber (°C); M_{CO2} is the molecular weight of CO_2 (44.01 g); and DW is the dry mass of the leaf litter sample (g). When R_{LL} was very small, the resolution of the IRGA (2–3 ppm) was insufficient to measure a clear increase in the CO_2 concentration. Thus, when the IRGA measurements indicated increases in the CO_2 concentration of less than 3 ppm in the measurement period (5 minutes), R_{LL} was assumed to be 0 $mgCO_2\ kg^{-1}\ h^{-1}$.

3 R_{LL} measurements

(a) *Vertical spatial variation in R_{LL} inside the L layer*

To evaluate the relationship between R_{LL} and WC among species, we

measured the R_{LL} and WC of the seven litter species from August 4 to 6, 2009. Measurement time was set during the daytime period (12:00 to 16:00) to minimize changes in temperature. The mean temperature in the chamber was 30.1°C. Changes in temperature during the measurement period were within ± 1.5°C. Leaf litter samples of *Qs* were collected from the deciduous forest floor, and these of *Cs*, *Le*, *Mt*, *Qm*, *Qg*, and *Ii* were collected from the evergreen forest floor (Fig. 1a). The ground at the evergreen forest was relatively flat and the thickness of the L layer was approximately 3 cm. In contrast, the terrain of the deciduous forest was complex with steep slopes, which induced heterogeneous thickness in the L layer and litter accumulations in a valley. Therefore, we collected leaf litter from the L layer to approximately 3 cm in the valley. To evaluate the effect of vertical position in the L layer on R_{LL} and WC, we divided the L layer into three layers (top, middle, and bottom) and obtained three leaves from each layer. We equally divided the L layer into three layers. Thus, thickness of one layer was about 1 cm. Care was taken to ensure that the selected leaves were retaining original form; no obvious symptoms of physical disintegration. After sampling, the CO_2 efflux from the sample (three leaves) was measured immediately using the chamber system in the field. The total numbers of measurements made in each layer were 5 and 7, for *Qs* and the others, respectively.

(b) *Temporal variation in* R_{LL}

Leaf litter samples of 3 species (*Ce*, *Le*, and *Mt*) were collected from the evergreen forest floor in November 2009. To obtain mean WC and R_{LL} in the L layer, 10 dead leaves were formed into one leaf litter stack (Fig. 1b). We prepared two leaf litter stacks each species. Total six leaf litter stacks were fixed to forest floor using wire pins

(diameter 2 mm) in November 2009. To examine the temporal changes in R_{LL} according to changes of WC among 3 species, at nine months after setting of leaf litter stacks, we measured WC and R_{LL} on 4 and 7 days (16 and 19 in August 2010) after rainfall (41.0 mm day^{-1}), respectively. The WC and R_{LL} were measured from one leaf separated from a set of 10 dead leaves composing leaf litter stack. The WC and R_{LL} were averaged from 10 dead leaves composing one leaf litter stack. The mean temperature in the chamber was 32.3°C. Changes in temperature during the measurement were within ± 1.5°C.

4 Sample treatment after R_{LL} measurements

After each R_{LL} measurement, litter samples were immediately enclosed in plastic bags. The fresh weight of leaf litter was measured in the laboratory within 24 h after sampling. Leaf litter samples were oven dried at 60°C for 48 h, and WC was calculated using

$$WC = \frac{(FW - DW)}{DW}, \quad (2)$$

where FW is the fresh mass of the leaf litter sample (g), and DW is the dry mass of the leaf litter sample (g). The area of leaf litter was measured with a LI-COR LI-3000A leaf area meter (Lincoln, NE, USA). Total C and N contents were measured using the combustion method in an NC-analyzer (NC-900, Sumitomo Chemical Co., Osaka Japan). Nutrients were determined from five samples randomly selected at each layer in each species.

Results

Values of *WC*, R_{LL}, and the C:N ratio inside the L layer clearly differed in association with their vertical position in the leaf litter (Fig. 2). Both *WC* and R_{LL} were significantly higher in the lower layers (Tukey's HSD, $p < 0.05$). Across all seven species, the C/N ratios of the bottom layer were lower than those of the top layer. The differences between the bottom and top layer of each species were significant (Tukey's HSD, $p < 0.05$) except for *Qs*. There was no significant difference in the variations in R_{LL} and *WC* between species, whereas there was a significant difference in the C:N ratio between species (one-way ANOVA, $p < 0.001$).

Even though the R_{LL} measurements were conducted under constant temperature (30.1 ± 1.5°C), R_{LL} had large variations that followed the *WC* variations (Fig. 3). The ranges in R_{LL} and *WC* of the seven species (*Qs*, *Cs*, *Le*, *Mt*, *Qm*, *Qg*, and *Ii*) were 40–1568, 0–2356, 19–1398, 0–1493, 38–1813, 0–1245, and 0–1658 $mgCO_2\ kg^{-1}\ h^{-1}$, and 0.19–2.12, 0.13–1.86, 0.14–1.93, 0.04–2.29, 0.17–2.66, 0.14–2.92, and 0.14–2.58 $g\ g^{-1}$, respectively. The value of R_{LL} was occasionally near zero below an *WC* value of 0.3 $g\ g^{-1}$. Across all seven species, R_{LL} was positively correlated with *WC* ($p < 0.001$), and the relationship did not differ significantly among the seven species (analysis of covariance, $p = 0.07$).

The temporal variation in mean *WC* among the three species was different (Fig. 4) and associated with the specific leaf surface area (*Cs*: 87.4, *Mt*: 81.1 and *Le*: 69.4 $cm^2\ g^{-1}$). The mean *WC* values of *Cs*, *Mt*, and *Le* 4 and 7 days after rainfall were 0.22–0.12, 0.36–0.21, and 0.82–0.16 $g\ g^{-1}$, respectively. Compared with thinner leaf litter (e.g., *Cs*), thicker leaf litter (e.g., *Le*) dried more slowly. Following the variation in *WC*, R_{LL} varied temporally among the three litter species. The mean R_{LL} values of *Cs*,

Mt, and *Le* 4 and 7 days after rainfall were 109–100, 253–94, and 562–81 mgCO_2 kg^{-1} h^{-1}, respectively. At 4 days after rainfall, the mean R_{LL} of the thicker leaf litter (e.g., *Le*) was 5.2 times as large as that of the thinner leaf litter (e.g., *Cs*). These mean R_{LL} similarly varied within range of R_{LL} seen on Fig 3.

Discussion and Conclusion

The measured R_{LL} in all seven species had large range, from zero to 2356 $mgCO_2\ kg^{-1}\ h^{-1}$, with a mean value of 546 $mgCO_2\ kg^{-1}\ h^{-1}$ (Fig. 3). Dilly and Munch (1996) reported that the R_{LL} of black alder litter ranged from approximately 100 to 700 $mgCO_2\ kg^{-1}\ h^{-1}$ at 22°C when WC was 2.5 $g\ g^{-1}$, and that it temporally varied during the course of decomposition. Coxson and Parkinson (1987) showed that the R_{LL} of aspen woodland litter ranged from approximately 50 to 550 $mgCO_2\ kg^{-1}\ h^{-1}$ at 18°C when WC ranged from 0.3 to 2.7 $g\ g^{-1}$. Their ranges included the average values of this study. However, our maximum R_{LL} was larger than theirs. We expect that their ranges of R_{LL} would be limited due to the laboratory experiments under a specific environment conditions (e.g., WC and temperature). Our maximum R_{LL} of each species (1245–2356 $mgCO_2\ kg^{-1}\ h^{-1}$) means that 1.6–3.1% of the substrate could be consumed by respiration only in one day, assuming that the carbon ratio in leaf litter is 0.5. On the other hand, even at high temperature, R_{LL} widely varied and could reach near zero under specific spatial and temporal condition (Figs. 3, 4). Therefore, large spatial and temporal changes in R_{LL} could occur in the L layer, and this R_{LL} variation would have a high potential to influence the spatial and temporal variation in soil respiration and heterotrophic respiration.

The magnitude of R_{LL} was strongly influenced by WC (Figs. 3, 4) and WC varied both spatially and temporally. First, focusing on the cause of WC variation inside the L layer, WC was highly related to the vertical position of leaf litter within the L layer (Fig. 2). The upper layer tended to be drier than the lower layer. As a result, R_{LL} widely varied between the top and bottom layers and followed the distribution of WC. Taylor and Parkinso (1988) indicated that the upper layer of the L layer was drier

under repeated drying and wetting cycles because this layer was exposed on the surface and the lower layer dried more slowly. Such vertical distribution in *WC* inside the L layer would affect the magnitude of integrated R_{LL} among layers. As a result of differing moisture histories among layers, a gradient of the degree of decomposition presented by the C:N ratio would occur within the L layer (Fig. 2).

Second, *WC* variation was related with leaf litter thickness (Fig. 4). The larger the specific surface area of substrate (e.g., the thinner leaf litter), the faster it dried, as is well known in the field of fire science (Fosberg 1971). Such physical characteristics of litter species affect the wetting and drying cycle of *WC* and exhibit different temporal variations in R_{LL} among litter species. And, our results showed that the response of R_{LL} to *WC* was similar among litter species (Fig. 3) despite interspecies differences in chemical quality (C:N ratio). From these results, we speculated that the moisture history of a substrate would finally result in difference of the annual R_{LL} and the decomposition rates between plant species. Virzo De Santo et al. (1993) also reported that the higher ability of leaf litter to retain water would result in the higher decomposition rate. The finding of a relationship between decomposition rate and moisture history was difficult due to many technical aspects. To understand the decomposition process in the forest floor, it is important to monitor moisture conditions in the litter itself, while taking into account physical environments as identified above (position and thickness of leaf litter).

Interest is increasing in the short-term factors that control heterotrophic respiration because of the potential for mitigating climate change, including precipitation and temperature. After rainfall, R_{LL} decreases with drying leaf litter, and the R_{LL} of all species reached near zero below *WC* of 0.3 g g^{-1}. As a result, instantaneous

R_{LL} showed a wide distribution even at the same temperature condition. Direct R_{LL} measurement, a measure of microbial activity, can indicate dynamic changes in decomposition processes responding to variations in environmental factors. Our data suggest that history of such environmental condition result in interspecies differences of the decomposition rate. On the other hand, many mass loss studies reported that differences in litter quality between plant species influence the decomposition rate (Hobbie et al. 2006; Salinas 2011). Microbes are directly responsible for majority of litter decomposition and their biomass and community structure could be influenced by the quality of individual plant species (Bardgett and Walker 2004; Ayres et al. 2006). To integrate the effects of environmental conditions and litter quality on decomposition processes, cross-measurement and validation of R_{LL} and microbial composition are required.

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Figure legends

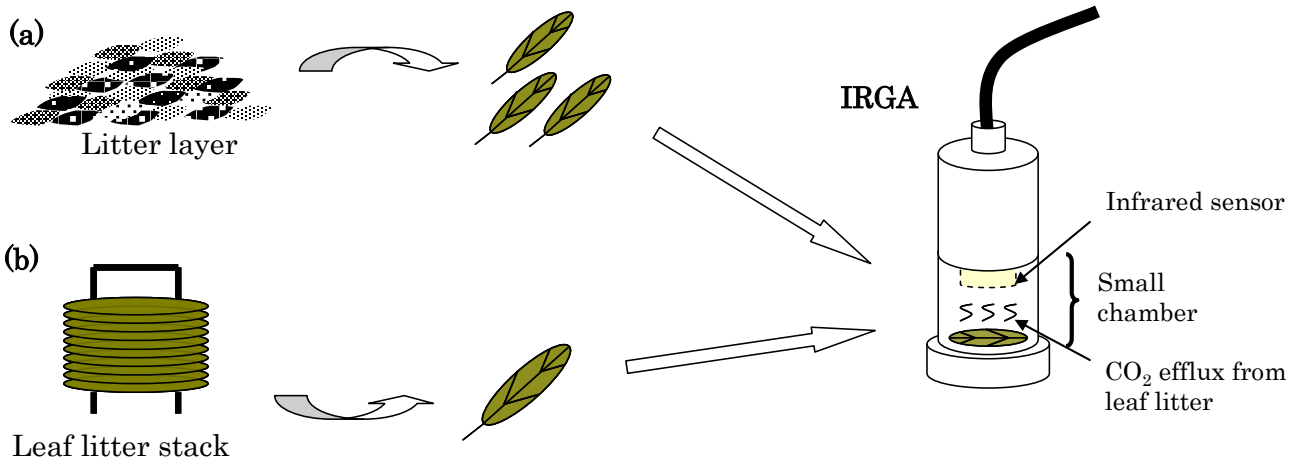
Fig. 1 Illustration of R_{LL} measurements. Measurements of R_{LL} were conducted by sampling leaf litter from (a) seven species and (b) three species. (a) The L layer was categorized into three layers, and R_{LL} was measured from three leaves in each layer. (b) A set of 10 dead leaves formed into vertical stacks was fixed to forest floor using wire pin, and R_{LL} was measured from a single leaf litter separated from the leaf litter stacks.

Fig. 2 Vertical spatial variation in the mean R_{LL}, WC, and C:N ratio inside the L layer (top, middle, and bottom layers) among the seven species. Bars indicate standard error. Different letters on the bar indicate significant differences among three layers (Tukey's HSD, $p < 0.05$).

Fig. 3 Relationships between R_{LL} and WC of the seven species.

Fig. 4 Temporal variation in mean R_{LL} and WC among three species, 4 to 7 days following rainfall (41.0 mm day^{-1}), measured in August 2010. Mean R_{LL} and WC were calculated from 10 dead leaves composing one leaf litter stack (Fig. 1b). Bars indicate standard error. Closed circles indicate the relationships between R_{LL} and WC as seen in Fig. 3.

M Ataka Figure 1



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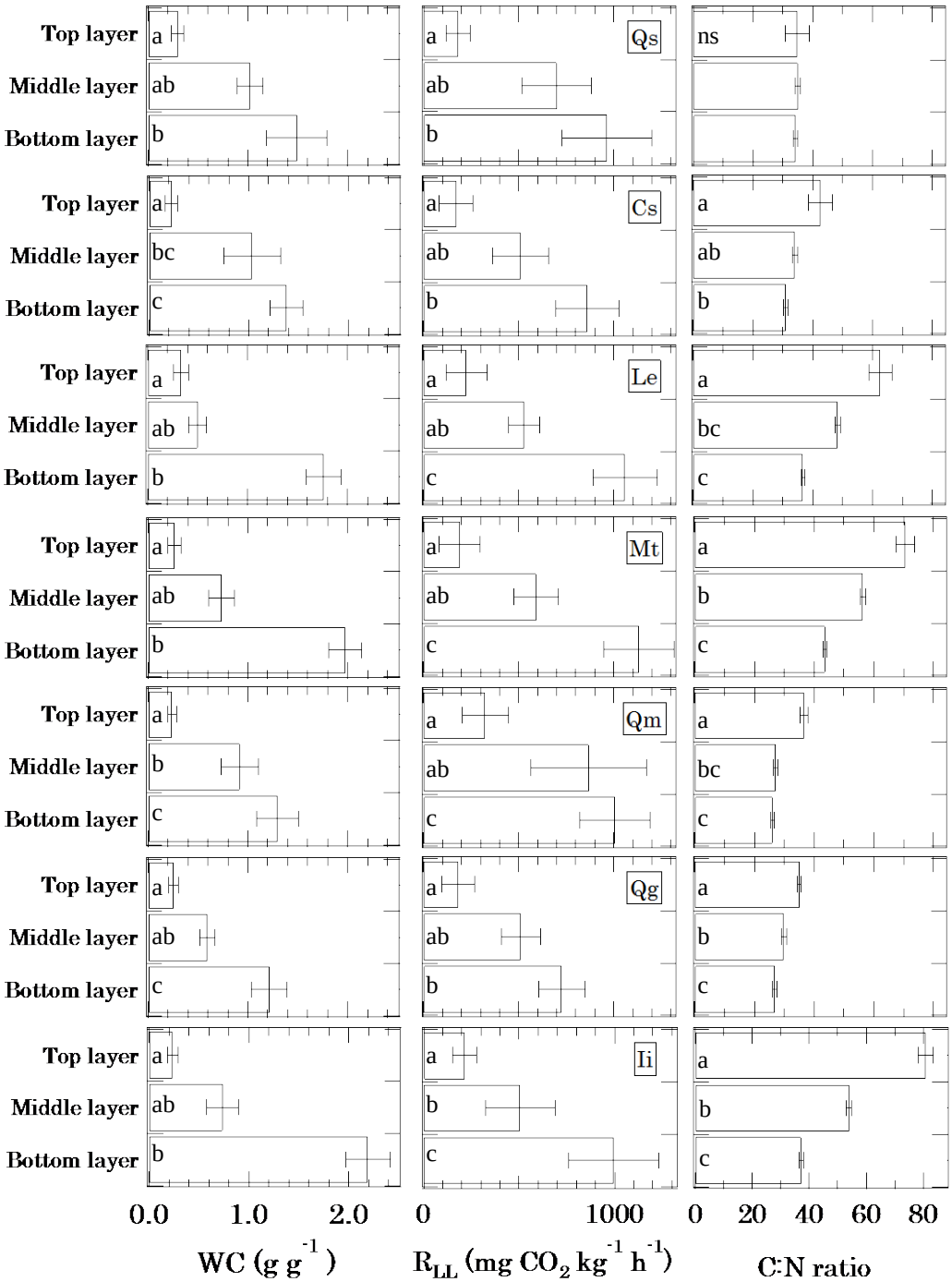
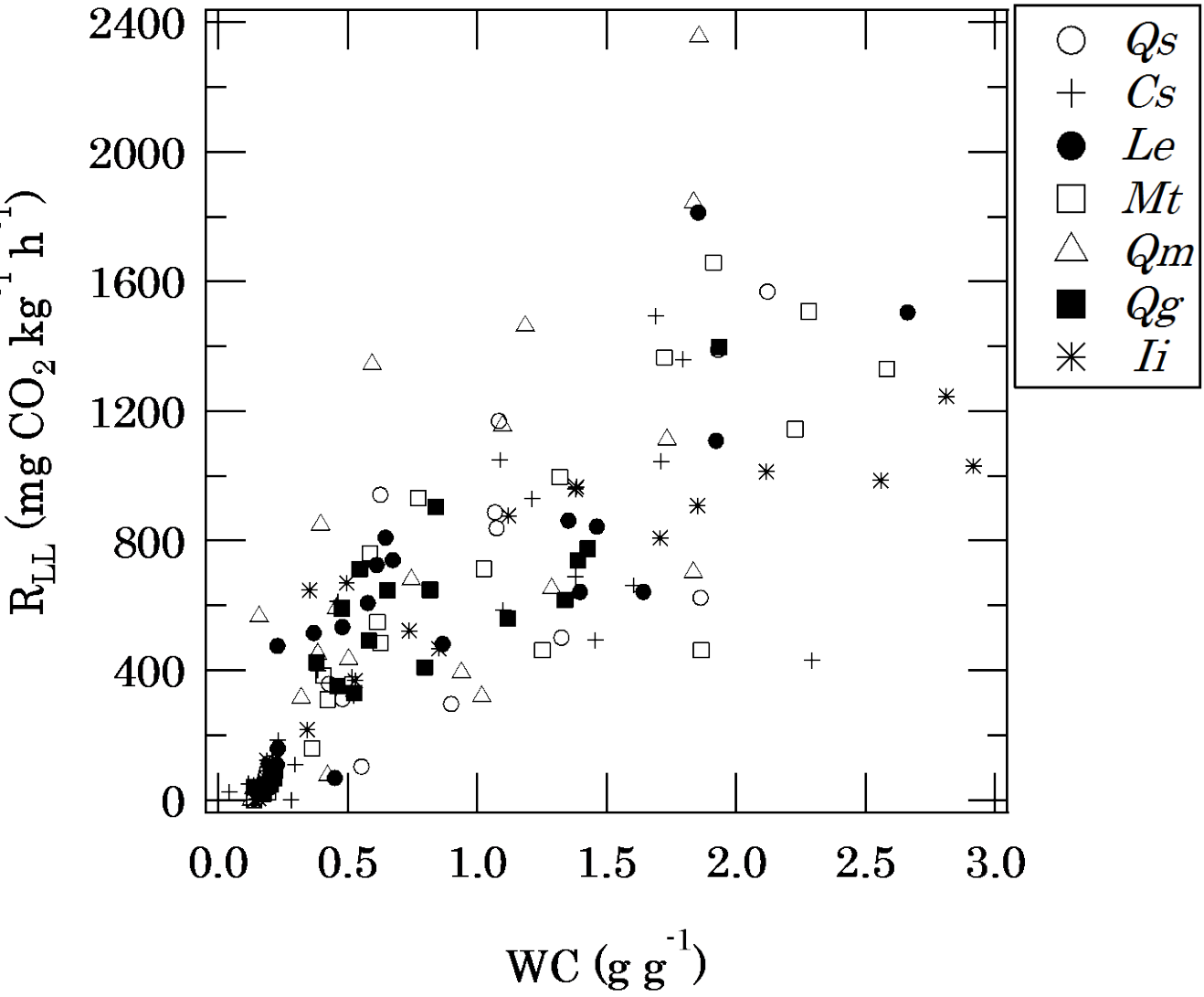


M Ataka Figure 3



M Ataka Figure 4